REPRODUCTIVE CYCLE OF THE SURF CLAM, SPISULA SOLIDISSIMA, IN OFFSHORE NEW JERSEY

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Atlantic surf clams, *Spisula solidissima* (Dillwyn), were collected from offshore New Jersey during a three and one-half-year period to obtain their gonads for histological treatment in a study of the annual reproductive cycle. Documentation of the annual reproductive cycle on the basis of gonad distention (Westman and Bidwell)[1] and excision of gametes (Allen, 1951, 1953; Schechter, 1941) is incomplete and fragmentary. Neither gonad distention nor excision of gametes assesses the events of gamete development within the gonad. Also, parasites are a possible source of error if the technique of observing gonad distention is used. I have seen infected surf clams with distended gonads when those of uninfected individuals were shrunken. Gonad color has been used as an indicator of sex and gonad development of the sea scallop, *Placopecten magellanicus* (Posgay and Norman, 1958; Merrill and Burch, 1960). The color of surf clam gonads containing mature sex products, however, is not consistent. Ovaries of females are sometimes pink, but may also be white, as are the testes (Schechter, 1941).

Periodic histological examinations of gonad tissue during several successive years has been a valuable method of determining the annual frequency and duration of the reproductive cycle in many marine invertebrates (Giese, 1959). The reproductive cycles of the soft-shelled clam, *Mya arenaria* (Pfitzenmeyer, 1962, 1965; Shaw, 1962, 1965; Ropes and Stickney, 1965) have been recently established by describing the cytological events within the gonad. Such events within the gonads of surf clams from an area of intensive fishing off the New Jersey coast have been related to water temperature. The present study of seasonal gonad development was undertaken to determine the annual frequency and duration of spawning—information basic to understanding larval occurrence and time of setting of juvenile surf clams.

MATERIALS AND METHODS

Surf clam gonads were collected from port landings (1962 and 1963) and commercial and research vessels (1964 and 1965). In all years, samples were taken as soon as practicable after the clams were removed from the water, because the surf clam readily reacts to artificial spawning stimuli (Stickney, 1963) and some released sex products soon after capture. All samples were from the vicinity of Barnegat Lightship and were caught by hydaulic dredges operating at depths of 18 to 32 meters. A sample was taken monthly during the winter and biweekly during the spring, summer, and fall. Each sample comprised 25 live clams with shells 120 mm. long or longer. The portion of the gonad ventrad to the heart was removed after fixation of the entire visceral mass in Bouin's solution, thereby preventing the loss of eggs and sperm, and minimizing the possible variability in development within a single gonad. Standard histological techniques were employed to prepare sections 7 μ thick for staining with Delafield's hematoxylin and eosin.

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[1] Westman, J. R., and M. H. Bidwell, 1946. The surf clam. Economics and biology of a New York marine resource. State of New York Conservation Dept. Unpublished manuscript on file at Bureau of Commercial Fisheries Biological Laboratory, Oxford, Maryland 21654.

After microscopic examination of the section, each specimen was assigned to a category of gonad development. The proportions of clams in each category, regardless of sex, were recorded for individual samples and the samples were combined each month to simplify presentation. In graphic presentations of the results, the combined data are plotted at a date midway between the sample dates.

The possible influence of temperature on gonad development and spawning was considered. Surface and bottom sea-water temperatures at Barnegat Lightship were obtained from Chase (1965, 1966) for 1962 and 1963 and from unpublished records for 1964 and 1965.

Anatomy and Spawning

Male and female surf clams are distinguishable by microscopic examination of the gonads because they are unisexual or dioecious (Coe, 1943). Hermaphroditism is rare and then is apparently a developmental accident (Ropes, 1966).

The gross features of a surf clam's reproductive anatomy include anastomosing gonadal alveoli which lie ventrad to the pericardial chamber and overlay the dark brown digestive gland or liver mass, and surround the coiled intestine. In the distended gonads before spawning, the root-like alveoli are crowded close to each other and are filled with "late ripening" and "ripe" sex cells; their connective tissue walls are stretched thin; and they occupy much of the visceral mass. After spawning the alveoli contract, their walls thicken, and mesenchyme is interspersed between them; the dark brown digestive gland is then the most prominent organ and the visceral mass is flaccid.

The alveoli lead into a pair of gonoducts, each of which has an enlarged portion that serves as a reservoir for ripe sex cells before spawning (Stickney, 1963). The gonoducts terminate at the genital apertures on minute papillae that protrude from the surface of the posterior foot retractor muscle on each side of the visceral mass.

The passage of water for respiration and digestion conducts sex cells from the clam into the surrounding water during spawning. Water drawn through the incurrent siphon flows into the infrabranchial chamber, around the gills, past the genital papillae, into the epibranchial chamber, and then out through the excurrent siphon. Spawning is often accompanied by rhythmic contractions of the adductor muscles which pull the two valves together. Gametes are either emitted into the water by the muscular activities or flow out. Ovocyte maturation follows spawning and fertilization (Costello *et al.*, 1957; Stickney, 1963) but meiosis occurs in the gonads of male surf clams and functional sperm are developed before spawning.

Categories of Gonad Condition

In this study the more or less continuous reproductive process was divided into five phases as described below. The demarcation between phases is not sharp—the divisions are convenient rather than natural.

Female gonads

1. *Early active phase*

In the early active phase ovogonia appear at the periphery and are embedded in the alveolar walls, often before the gonads are completely empty of ripe ovocytes. The round and oval nuclei of ovogonia contain distinctly basophilic nucleoli and the nucleoplasm has thin, irregularly shaped, dark-staining threads (Fig. 1). Cytoplasm surrounds the nuclei but is indistinct and of irregular shape. The ovogonia are possibly undergoing the pre-meiotic stages similar to those described for the desert snail, *Eremina desertorum* (Fahmy, 1949) and the soft-shelled clam, *Mya arenaria* (Coe and Turner, 1938). The alveolar walls are not completely contracted and lumina are evident in most gonads.

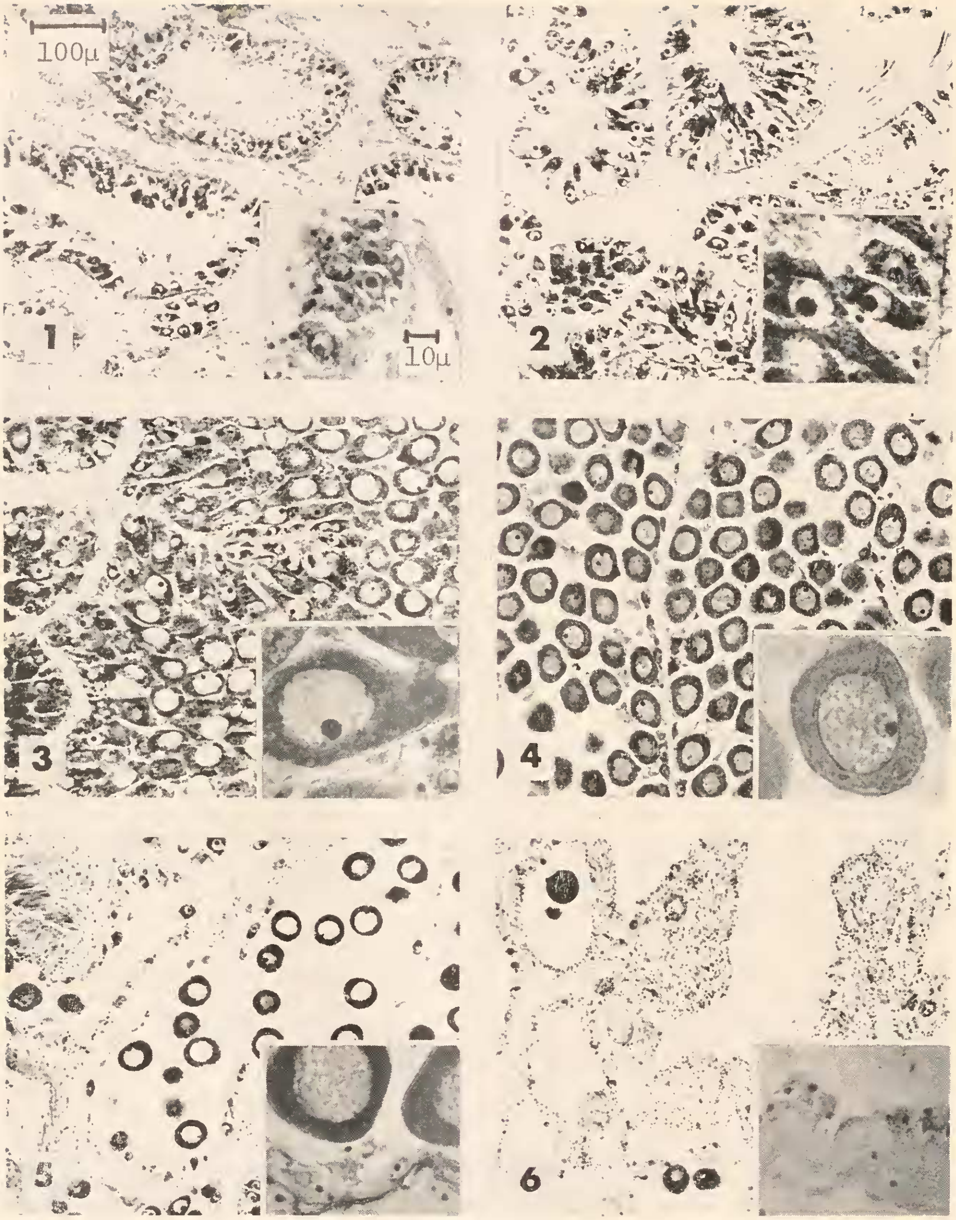
The early ovocytes also have mostly round and oval nuceli containing basophilic nucleoli, but the nucleoplasm is homogeneous and almost clear (Fig. 2). The ovocytes lie at the periphery of the alveolar walls and the cytosome extends into the lumen of the alveolus, where a rounded cap is formed. The shape of the ovocytes may be square, triangular, cylindrical, or hemispherical. All of these ovocytes are attached to the basement membrane by a stalk. The diameters of the nuclei range from 5 to 20 μ and average 11.1 μ.

2. *Late active phase*

Ovocytes in the late active phase are larger than early ovocytes and many are round (Fig. 3). The nuclei contain basophilic nucleoli and the nucleoplasm is homogeneously granular. The nuclei, surrounded by cytoplasm, are the most conspicuous characteristic of the cells. Some ovocytes are attached to the basement membrane of the alveoli by a thin stalk, but most are free in the lumina. The basement membrane is thin—apparently due to the increased volume of cells within the alveoli. The diameters of the nuclei range from 14 to 32 μ and average 24.1 μ.

3. *Ripe phase*

In ripe clams, ovocytes are free in the lumina of the alveoli. The vitelline membrane contains the cytoplasm and a large nucleus (Fig. 4). These ovocytes are very similar to those in the late active phase except for the presence of prominent amphinucleoli (Allen, 1953). Each amphinucleolus consists of an almost transparent, granular nucleolus and a small opaque, basophilic nucleolinus. Ripe gonads typically have a dense appearance because the alveoli are crowded together and are filled with large ovocytes. The diameters of the nuclei range from 22 to 33 μ and average 28.5 μ.



FIGURES 1–6.

FIGURE 1. Section of gonad tissue from a female surf clam, early active phase of the first annual reproductive cycle. All of the large photomicrographs are reproduced at the same magnification and a scale (100 μ) is provided. The small photomicrographs inserted in the lower right-hand corner of each figure are enlargements of portions of the gonad all at the same magnification and a scale (10 μ) is provided. Collection date: 21 January 1964.

4. *Partially spawned*

A few large, ripe ovocytes are free in the lumina of some alveoli of partially spawned clams; other alveoli are completely void of ripe ovocytes (Fig. 5). Ovogonia and early ovocytes appear in the contracted and thickened alveolar walls. The spaces between alveoli contain mesenchyme and the whole gonad has a loose, flaccid appearance. In some clams, ripe ovocytes are being cytolyzed.

5. *Spent*

In typical spent clams, the open lumina of alveoli are usually void of ripe ovocytes. The thickened alveolar walls contain ovogonia and early ovocytes (Fig. 6). Mesenchyme occurs in the spaces between the loosely arranged alveoli.

Male gonads

The criteria for the five categories of gonad condition in the male are presented below:

1. *Early active phase*

Clams in the early active phase contain cells undergoing the initial meiotic stages of development. Darkly stained spermatogonia are in the thickened alveolar walls (Fig. 7). Primary spermatocytes about 3 to 4 μ in diameter proliferate toward the lumina from a close contact with the alveolar walls and form single cell columns (Fig. 8). Their large, round and oval nuclei are surrounded by thin irregularly shaped cytoplasm. Two basophilic nucleoli within some cells indicate that cell division is taking place. The nucleoli are less basophilic and smaller than those in the earliest ovocytes.

2. *Late active phase*

The remaining spermatogenic stages are seen in clams in the late active phase. Secondary spermatocytes of about 2 to 3 μ in diameter with dark basophilic chromatin threads that nearly fill the nuclei are numerous and the surrounding cytoplasm is irregular in shape and very indistinct (Fig. 9). Small and strongly basophilic spermatids measuring about 1.5 μ in diameter form dense masses near the centers of the alveoli. A transformation of the spermatids results in the appearance of sperm in the lumina. The sperm form weak columns with the tails oriented toward the centers of alveoli. The sperm heads are about 1 μ in diameter.

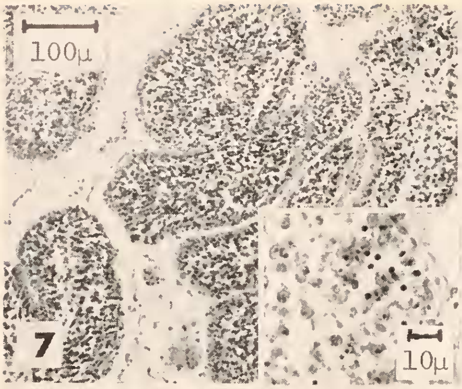
FIGURE 2. Same from a female surf clam, early active phase, showing enlarging ovocytes. Collection date: 18 February 1964.

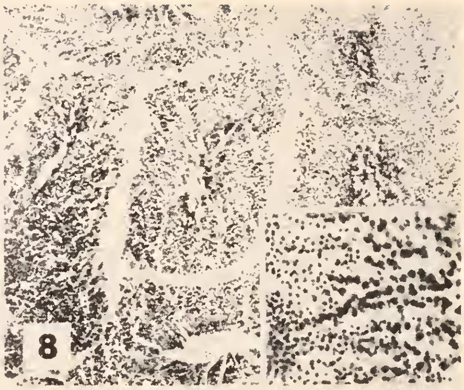
FIGURE 3. Same, from a female surf clam, late active phase, showing large oval ovocytes. Collection date: 18 February 1964.

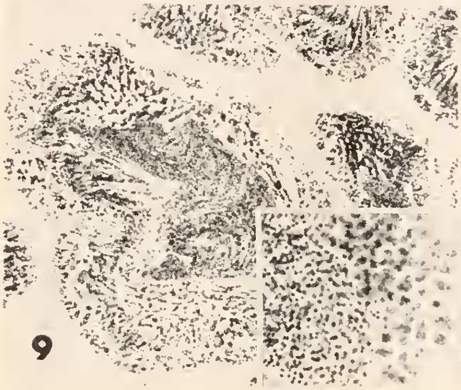
FIGURE 4. Same, from a female surf clam, ripe phase. Collection date: 26 June 1964.

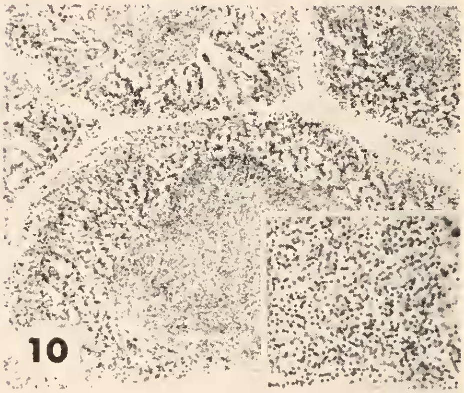
FIGURE 5. Same, from a female surf clam, partially spent phase. Collection date: 28 August 1964.

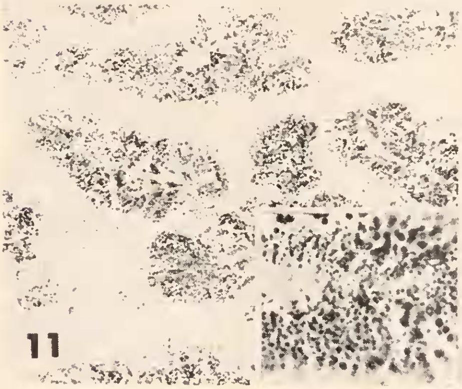
FIGURE 6. Same, from a female surf clam, spent phase. Collection date: 13 August 1964.

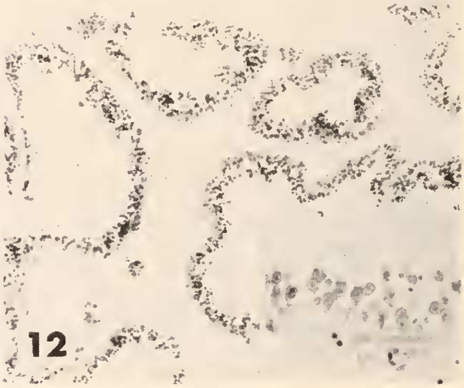












FIGURES 7–12.

FIGURE 7. Section of gonad tissue from a male surf clam, early active phase of the first annual reproductive cycle. Collection date: 21 January 1964.

FIGURE 8. Same, from a male surf clam, early active phase, spermatozoa form columns. Collection date: 18 February 1964.

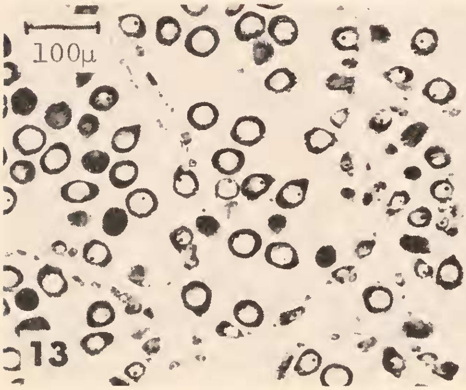
FIGURE 9. Same, from a male surf clam, late active phase. Collection date: 3 June 1964.

3. *Ripe phase*

Mature sperm form dense masses in the alveoli of clams in the ripe phase (Fig. 10). The sperm appear to be swirling in the centers of some alveoli, in others their tails are oriented toward the centers of alveoli, and in still others they form a homogeneous mass. Cells in early stages of spermatogenesis at the periphery of alveoli are much less numerous than the sperm.

4. *Partially spawned phase*

Partially spawned male clams still contain spermatozoa within the centers of alveoli, but they are substantially less numerous than in ripe clams (Fig. 11). The alveolar walls are compressed and thickened. Like the ovogonia and early ovocytes at this stage, spermatogonia and primary spermatocytes are developing along the basal membrane before most gonads are completely void of spermatozoa.



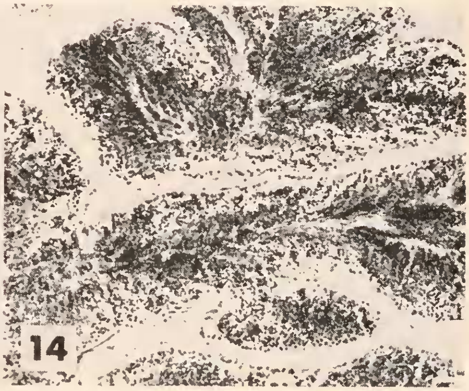


FIGURE 13. Section of gonad tissue from a female surf clam, ripe phase of the second annual reproductive cycle. Collection date: 24 September 1964.

FIGURE 14. Section of gonad tissue from a male surf clam, ripe phase of the second annual reproductive cycle. Collection date: 24 September 1964.

5. *Spent phase*

The alveoli of spent male clams contain no spermatozoa or very few and the lumina are characteristically open (Fig. 12). Primary spermatogonia are proliferating from the alveolar walls.

SECOND ANNUAL CYCLE

A second annual maturation of New Jersey surf clams was observed during three of the four years and was essentially a repetition of the sequence in gonad conditions already presented. The second maturation seemed to be of minor

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FIGURE 10. Same, from a male surf clam, ripe phase, a dense mass of spermatozoa is formed. Collection date: 15 July 1964.

FIGURE 11. Same, from a male surf clam, partially spawned phase. Collection date: 29 July 1964.

FIGURE 12. Same, from a male surf clam, spent phase. Collection date: 29 July 1964.

importance, however, since fewer ovocytes appeared in the gonadal alveoli (Fig. 13). Counts of the number of ovocytes in 1.25 mm.^{2} of gonadal tissue sections of ripe clams from the two reproductive cycles in 1964 showed an average density of 44.2 ovocytes for 32 ripe clams from the first cycle and 26.4 ovocytes for 20 ripe clams from the second cycle. The sperm in male gonadal tissues also appeared to be less numerous during the second cycle (Fig. 14).

Annual Reproductive Cycles in Relation to Water Temperature

An account of the gonad conditions in 1514 surf clams and bottom water temperatures taken in the area sampled for clams is presented in chronological order. Gonad collections were initiated in June, 1962, and continued through 1965; water temperature data were available for the period 1962–65. Unless otherwise specified, all references to water temperature are for the bottom.

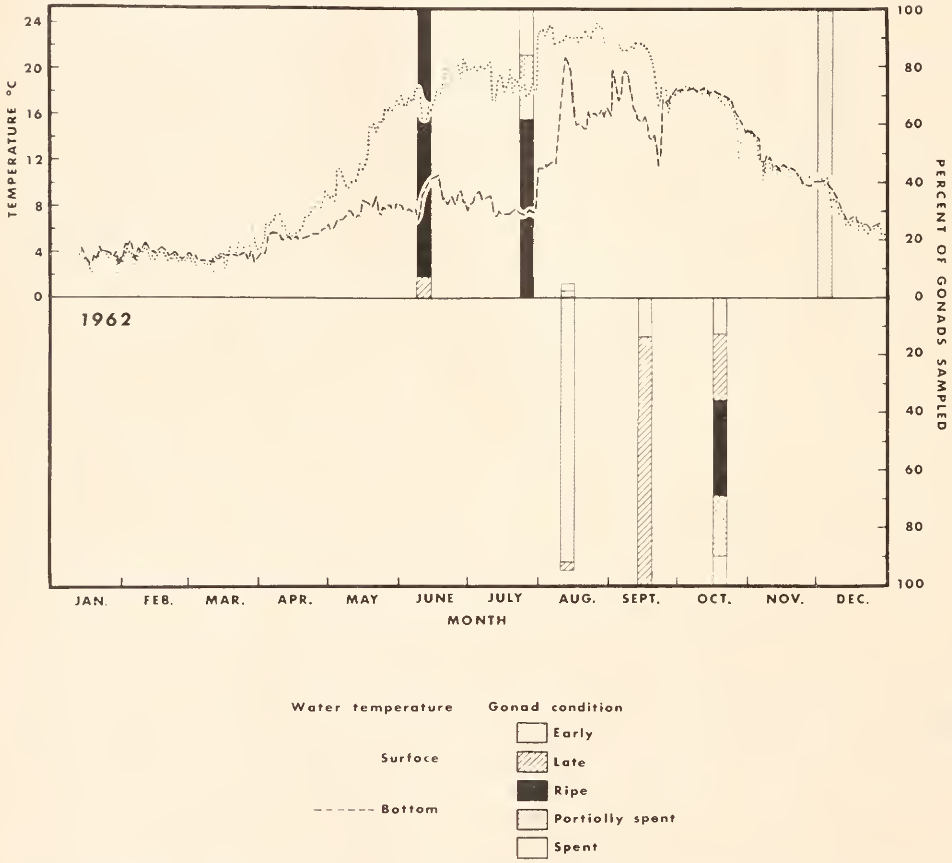

Figure 15. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1962. The bars above the centerline represent a single reproductive cycle and those below the centerline represent a subsequent cycle.

Reproductive cycle and water temperature in 1962

The June and July samples contained mostly ripe clams (Fig. 15). Spawning began by about mid-July when 37% of the clams were in the partially spawned and spent condition, and was completed by mid-August when 94% of the clams were in the early active phase. All clams were in the early and late active phases during September. All phases of gonad condition were represented in the October sample. A second spawning was apparent in mid-October when 32% of the clams were partially spawned and spent. All clams collected in early December were in the early active phase.

The temperatures were lowest (2.2° C.–5.2° C.) in late January, February, and early March. A warming trend followed, and 8° C. was reached by mid-May. The temperature reached 10.7° C. in mid-June, but most temperatures were between 7° C. and 9° C. during the 1½ months preceding the mid-July spawning. Spawning began 1 to 2 weeks before a rapid temperature rise, from 8° C. to 21° C., during late July to mid-August. Clams in the early active phase of a second reproductive cycle were most numerous when the temperature had reached its seasonal high (21° C.). The second spawning was in October, during a period when temperatures dropped from a high of 18° C. to about 10° C.

Reproductive cycle and water temperature in 1963

All of the clams were in the early active phase in January (Fig. 16). Gonads were in the late active phase in 4% of the clams by mid-February and in 56% of the clams by mid-March. Ripe clams constituted 92% of the mid-May sample and 98% of the mid-June sample. Spawning began in early July when 60% of the clams were partially spawned or spent. During August, 75% of the clams were still partially spawned or spent. The first annual spawning must have been completed by the end of August, because by mid-September 96% of the clams were in the late active and ripe phase. In mid-October collections, 28% of the clams were partially spawned and spent—evidence of a second spawning. Most (92%) of the clams were in the early active phase by early December.

Winter temperatures fell to a low of 2° C. during February. A warming trend after March (bottom temperatures are not available for March) was gradual and without marked fluctuations. The temperature on the bottom reached 10° C. by early June and 11° C. by late June. Temperatures reached 12° C. in mid-July. Spawning in July and August preceded a rapid rise in temperature from 9.6° C. to 18.9° C. during the early part of September. The beginning of a second reproductive cycle coincided with the rapid rise in temperature. The second spawning in October was during a period when temperatures dropped from 17° C. to about 15° C.

Reproductive cycle and water temperature in 1964

All clams were in the early active phase in January (Fig. 17); 63% were in the late active phase in February and this condition predominated in March and April. Gonads were ripe in 79% of the clams in May and in all of the clams in June. Spawning occurred in early July (43% of the clams were in the partially spawned and spent condition in mid-July). Fifty-three per cent of the clams were partially spawned and spent in mid-August and the rest were in the early active phase. A progressive development of the gonads during September and October was followed by a second spawning late in the year; 68% of the clams were partially spawned and spent in early November. In early December, 80% of the clams were in the early active phase.

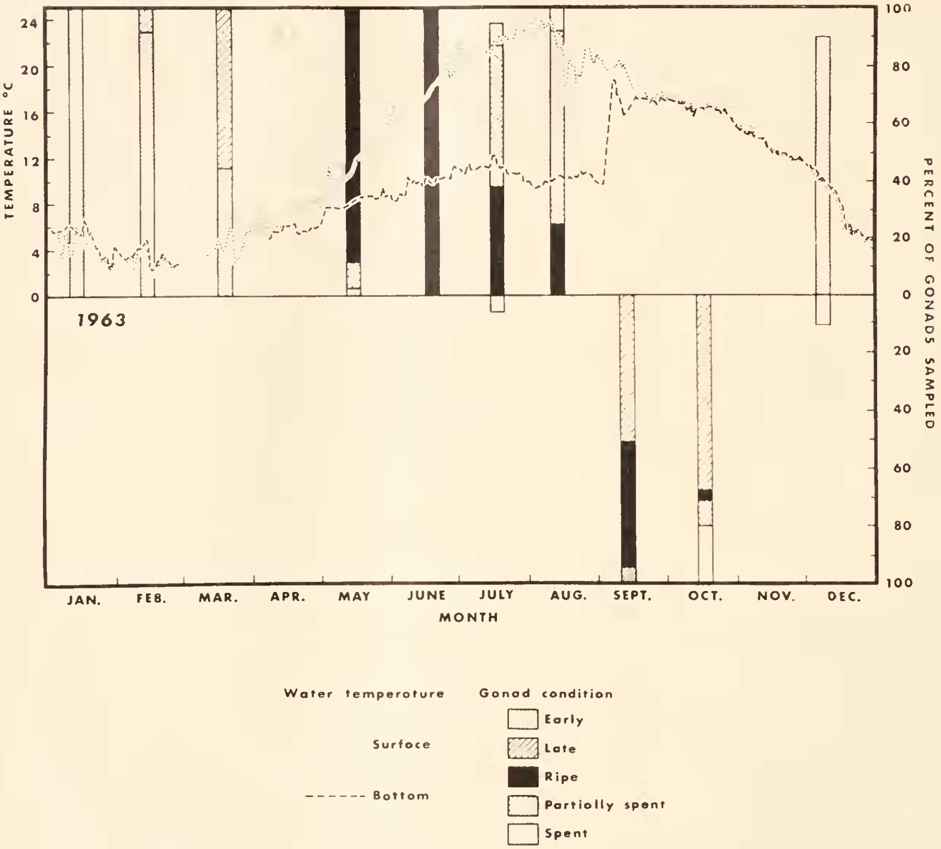

FIGURE 16. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1963.

The period of low winter temperature from January through March included a drop to 2° C. in February and was followed by a warming trend in April. In May and June the bottom temperatures fluctuated between 7° C. and 9° C. A temperature of 11° C. was reached in early July and was a possible inducement to spawning. All of the clams were completely spawned out in August after the rapid rise in temperature (7.4° C.–18.6° C.) during late July. The second reproductive cycle was underway in 47% of the clams after the rapid rise in temperature. The second spawning was during a period when temperature dropped from 16° C. to about 12° C.

Reproductive cycle and water temperature in 1965

All clams were in the early active phase during January and February (Fig. 18). The late active phase appeared in 76% and 62% of the clams during March and April, respectively. Ripe clams made up 94% of the late June sample and continued to predominate in the July, August, and September samples. In July and August only 7% to 11% of the clams were partially spawned and from mid-September to mid-October 29% to 52% of the clams were partially spawned or spent. Thus a mid-year spawning observed during the 3 previous years of the study was delayed 2 months in 1965. A few clams (7% to 13%) were in the spawning condition in late November and mid-December. From mid-October through December, however, many clams (48% to 93%) were in the early active phase. No second reproductive cycle was observed.

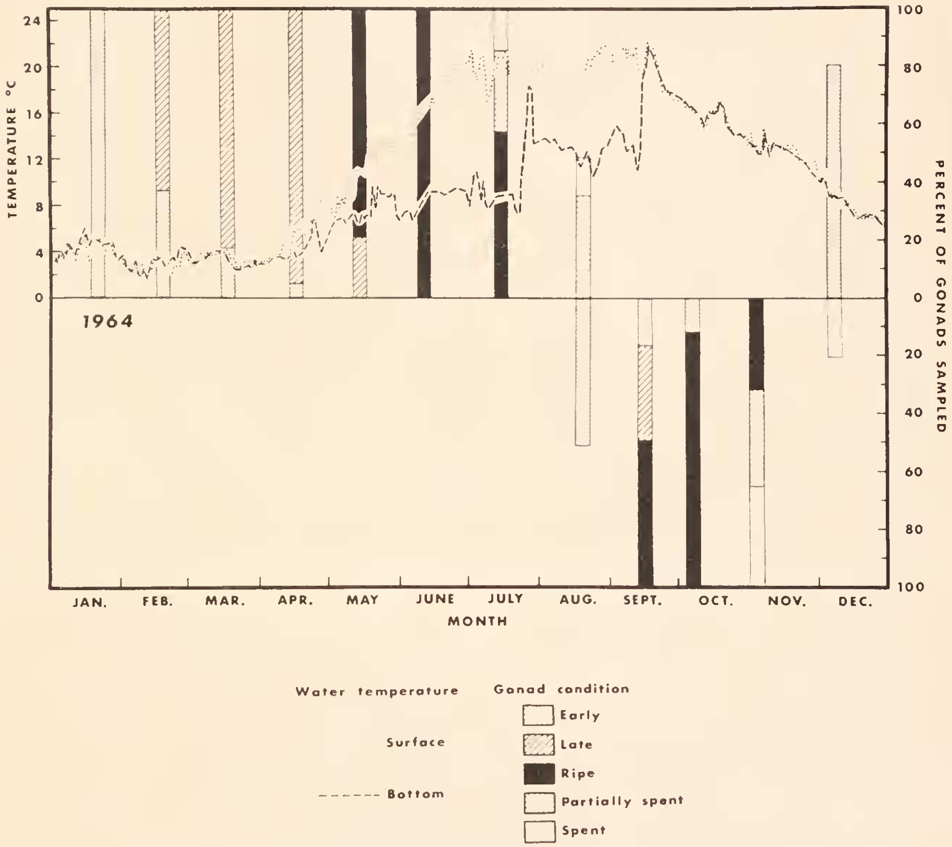

FIGURE 17. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1964.

Low winter temperatures were approximated from the surface observations because bottom temperatures were not available until early May. Warming to about 6° C. in May was followed by temperatures of about 8° C. in June and July; fluctuations of 2° C. occurred but the temperature did not exceed 10° C. Temperatures of 11° C. were recorded on three occasions in August. Temperature rose sharply from 10° C. to 18° C. in mid-September. Unlike the sequence in the 3 earlier years, spawning apparently occurred after the sharp rise in temperature.

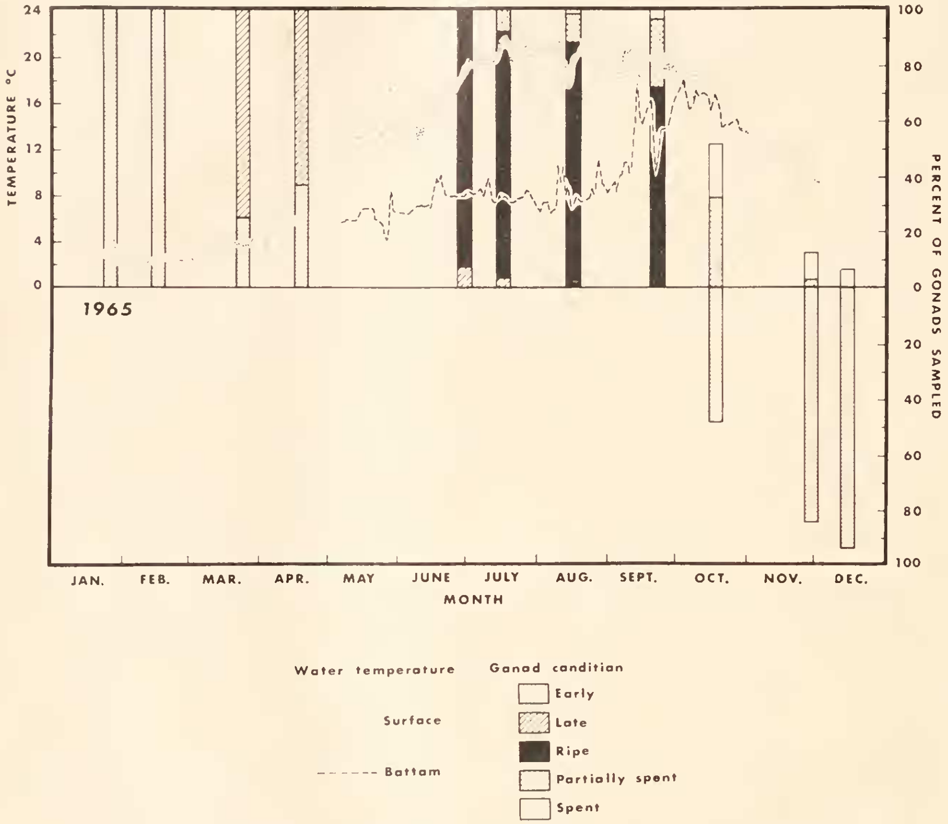

FIGURE 18. Gonad conditions of *Spisula solidissima* from New Jersey and sea-water temperatures at Barnegat Lightship in 1965.

DISCUSSION

In this study the term "reproductive cycle" includes the earliest detection of sex cells during periodic histological examinations of gonad tissue, the growth of female sex cells and multiplication of male sex cells which eventually fill the gonadal tubules, and the disappearance of sex cells from the tubules during the spawning period. The reproductive cycle can be separated into the gametogenic period (*i.e.*, the early, late, and ripe phases) and the spawning period (*i.e.*, partially spawned and spent phases). No period of inactivity was apparent in the sections of surf clam gonads, since sex cells for a succeeding reproductive cycle were detected in spent individuals (Figs. 6 and 12). In fact, separating the reproductive cycles of some marine invertebrates into an "inactive phase," "rest period," "quiescent period," or "vegetative phase" may only be a convenience (Ropes and Stickney, 1965). Biological processes maintaining life and early gametogenesis could very well be taking place during the inactive phase and be undetected by the histological technique used.

Examinations of the slide preparations of gonads provide an accurate basis for describing the reproductive cycle of surf clams from offshore New Jersey. Sex cell development began during December and, concurrent with the enlargement of the gonads, was followed by the occurrence of numerous partially spawned and spent clams during July and August each year from 1962 through 1964. A second maturation of sex cells followed the mid-year spawning, but gonad distention was minimal. Partially spawned and spent clams in the mid-October to early November samples in 1962 through 1964 was evidence of a second annual spawning. Although a biannual reproductive cycle may be typical for surf clams from offshore New Jersey during most years, a single reproductive cycle and spawning in 1965 was an important exception. The time and frequency of spawning each year, then, can vary.

Detection of a biannual reproductive cycle in surf clams from offshore New Jersey would be difficult without microscopic examinations of gonads throughout several calendar years. Westman and Bidwell (1946, see footnote 1) reported a mid-year spawning of surf clams from offshore Long Island, New York, by observing gonad distention and shrinking after spawning, but their method of visually determining gonad condition might not be precise enough to identify a second annual spawning, if one occurred. Allen (1951, 1953) observed a scarcity of eggs in surf clams from Woods Hole, Massachusetts, during 1 to 2 weeks in mid-summer coincident with a period of excessive heat. A possible explanation is that the clams had spawned or, since he continued to collect eggs for a 2- to 3-month period after mid-summer, these eggs may have been produced during a second annual reproductive cycle.

Temperature frequently influences the reproductive cycle and spawning of marine invertebrates (Giese, 1959; Loosanoff and Davis, 1963). During the gametogenic period, the surf clams in the beds off New Jersey were surrounded by gradually increasing, but fairly stable temperatures for the first six months in the three early years of the study. A progressive development of the gonads to a turgid and ripe state during the period of warming to temperatures of 12° C. or a little less preceded the first annual spawning. In 1965, however, the water temperatures during the gametogenic period were generally colder (8° C. or less) and more erratic (highs to 11° C.) than in the previous years. Gametogenesis was slightly delayed by the lower temperatures—94% of the clams were in the ripe phase by late June, 1965, whereas 100% were in the ripe phase by mid-June of 1962, 1963, and 1964.

Temperature was not clearly a stimulus to spawning of surf clams in their natural beds off New Jersey. Spawning by some clams did not accompany abrupt temperature changes in all 4 years, although more clams spawned before the abrupt temperature change in 1962–64 than in 1965. Spawning by some bivalves can be effectively delayed by holding them at low temperatures. Conversely, gonad development to a ripe condition has been hastened by holding bivalves in warm sea water.

The ripe bivalves have been spawned "out of season" and have produced normal larvae (Loosanoff and Davis, 1963).

I have held surf clams in 20° C. water from late February to mid April, 1967 and compared their gonadal development with that of clams from the parent population in Chincoteague Inlet, Virginia. Gonads of all clams in the inlet were in the late active phase in late February and remained in this condition until after April. Water temperatures during the experimental period gradually increased from 5° C. to 11° C. In contrast, 10 gonads from clams held in the warmed water were all in the ripe phase by mid-March. On 11 April, a female spawned spontaneously in one of the containers and 2 partially spawned individuals were found when gonad sections of 10 clams were examined. These three specimens, then, spawned without the stimulus of a thermal shock and were perhaps like the ripe individuals from the beds off New Jersey that spawned before an abrupt temperature change.

The surf clam apparently develops its gonads to a ripe condition within a short period of time, contains ripe sex cells for several months of the year, and responds readily to relatively simple spawning stimuli. A rapid gonad development may account for the report by Carson (1945) that the surf clams of the mid-Atlantic coast spawn in the spring and throughout the summer. Allen (1951, 1953) obtained eggs of New Jersey coast clams from early spring to late autumn. Schechter (1941) collected ripe surf clams from areas near Woods Hole, Massachusetts, throughout the summer. Loosanoff and Davis (1963) found morphologically ripe eggs and spermatozoa in surf clam gonads from mid-January to the end of June. Conditioning the clams in the early months of the year by placing them in warmed water produced ripe specimens. Later in the season, when the natural waters had reached 12° C., no conditioning was needed, and thermal stimulation alone was sufficient to induce spawning. In contrast, other species of bivalves in the laboratory require various physical and chemical stimuli such as electrical shocks, rhythmic changes in water temperature, the addition of ammonium hydroxide to the water or injected into the gonad, or an introduction of egg or sperm suspensions to the water to induce spawning—and even then some species do not respond (Galtsoff, 1961, 1964; Loosanoff and Davis, 1963; Stickney, 1964).

The importance of nervous and hormonal interrelationships in bivalves has been reviewed by Galtsoff (1961, 1964) and Giese (1959). Products of neurosecretory cells inhibit spawning, and bivalves become sensitive to environmental spawning stimuli after the cells disappear. Degeneration of the neurosecretory cells begins a few days before spawning. Nagabhushanam (1963a) recognized two types of neurosecretory cells in the cerebral and visceral ganglia of *Spisula solidissima.* The cells in surf clams appear morphologically similar to those in the oyster, *Crassostrea virginica*, and the mussel, *Modiolus demissus* (Nagabhushanam 1963b, 1963c, 1964). Experiments with the latter two species link the cells with the hormonal control of the gametogenic cycle and spawning. Stimuli such as low salinities, electrical shocks, and high temperature influenced the secretions.

Both Galtsoff (1961) and Stickney (1964) believed that ripeness, rather than specific temperature, influences the response of some bivalves to spawning stimuli. Ripeness and sensitivity to spawning stimuli seem to precede the natural spawning period of surf clams by many months. I classified surf clams from New Jersey as ripe for at least two months each year before the first annual spawning. Some were induced to spawn in late May and early June, 1965, by simply placing them in running sea water aboard a research vessel. At four locations where the clams were caught, the water temperature increased as little as 9.5° C. and as much as 11.5° C. from bottom to surface. Changes in hydrostatic pressure or shocks from being caught by the jet dredge might stimulate spawning, but none of the clams from a fifth location spawned when the temperature change was only 0.8° C. A response to the stimuli of an abrupt change in temperature, well in advance of the seasonal time of spawning, suggests that the hormonal control of spawning can be overridden in surf clams. Nevertheless, a minimum temperature threshold for a spawning response is probably necessary.

Sections of surf clam gonads from geographic locations other than the commercial fishing areas off the New Jersey coast were examined, since a biannual reproductive cycle and spawning may not be typical throughout their range. In monthly samples from a more northern habitat—Sagadahoc Bay, Maine—during May through September, 1962, only a single reproductive cycle was apparent. Partially spawned and spent clams in the August and September samples were evidence of a late summer and early fall spawning.

In other bivalves, the reproductive cycle changes with latitude. Pfitzenmeyer (1962, 1965) and Shaw (1962, 1965) observed a biannual reproductive cycle in soft-shell clams, *Mya arenaria,* from Chesapeake Bay, Maryland, the southern part of their range. Ropes and Stickney (1965) reported on a single annual cycle in soft-shell clams from areas north of Cape Cod, Massachusetts, and discussed the available evidence of a biannual cycle and spawning south of Cape Cod. Porter (1964), who described the seasonal gonadal changes in hard clams, *Mercenaria mercenaria,* from North Carolina, found two annual spawning periods. Both of these species apparently have only one reproductive cycle each year, but two in southern waters. The change in the breeding season with respect to latitude and an extension of the season as one goes south has been observed in many temperate marine invertebrates (Giese, 1959).

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SUMMARY

1. A biannual reproductive cycle was observed in *Spisula solidissima* gonads during 3 of the 4 years in which samples were taken from offshore New Jersey.

2. The biannual cycle was characterized by a major mid-year spawning and minor late-year spawning. A second annual reproductive cycle may be neither typical for surf clams throughout their geographical range nor always an annual event in clams from New Jersey.

3. A delayed spawning and single annual cycle in 1965 was related to colder environmental temperatures than were observed in the three earlier years of the study.

4. Abrupt temperature changes were not clearly a cause of spawning in the natural populations of surf clams. Partially spawned clams were found in the samples in advance of abrupt temperature changes. Temperature, however, clearly delays or hastens the gametogenic cycle and stimulates spawning of ripe surf clams in the laboratory.

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